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Research Article

Tracking Sumatran Tiger (*Panthera tigris sumatrae* Pocock, 1929) distribution in Gunung Leuser National Park: The influence of prey presence and environmental variables on habitat selection

M Hadi Saputra[1], Salmah Widyastuti[2], Wanda Kuswanda[2], R. Taufiq Purna Nugraha[2], Hendra Helmanto[1], Nunu Anugrah[3], U Mamat Rahmat[4], Rudianto Saragih Napitu[5], Andrinaldi Adnan[6], Iskandarrudin[6], Agus Purwoko[7], Pindi Patana[7]

1 *Research Center for Ecology and Ethnobiology, National Research and Innovation Agency, Jalan Raya Jakarta-Bogor Km 46, Cibinong, West Java 16911, Indonesia*
2 *Research Center for Applied Zoology, National Research and Innovation Agency, Jalan Raya Jakarta-Bogor Km 46, Cibinong, West Java 16911, Indonesia*
3 *Directorate of Species and Genetic Biodiversity Conservation, Directorate General of Natural Resources and Ecosystem Conservation, Ministry of Environment and Forestry, Jl. Jenderal Gatot Soebroto, Jakarta 10270, Indonesia*
4 *Public Relations Bureau, Ministry of Environment and Forestry, Jl. Jenderal Gatot Soebroto, Jakarta 10270, Indonesia*
5 *Directorate of Environmental and Forestry Prevention and Security, Directorate General of Law Enforcement, Ministry of Environment and Forestry, Jl. Jenderal Gatot Soebroto, Jakarta 10270, Indonesia*
6 *Gunung Leuser National Park Agency, Komplek Perkantoran Kementerian LHK Jln. Cut Nyak Dien, Km 1.2, Kel. Emperom Kec. Jaya Baru, Banda Aceh, Aceh, Indonesia*
7 *Faculty of Forestry, Universitas Sumatera Utara, Jl. Lingkar Kampus USU, Kampus 2 USU Bekala, Simalingkar A, Kec. Pancur Batu, Deli Serdang, Sumatera Utara 20353, Indonesia*

Corresponding author: Wanda Kuswanda (wand002@brin.go.id)

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Abstract

The Sumatran Tiger (*Panthera tigris sumatrae* Pocock, 1929) is a critically endangered tiger subspecies facing serious challenges such as land cover change and prey population declines. This study generated a species distribution model (SDM) of Sumatran Tigers in Gunung Leuser National Park (GLNP) on the island of Sumatra, Indonesia, by integrating predictive prey distribution data and environmental variables. The algorithms used are maximum entropy and random forest. Modeling results showed a positive correlation between the presence of prey animals and forest cover on Sumatran Tiger habitat suitability. Climatic factors and land cover directly affected prey animal distribution, while land cover and prey animal presence affected Sumatran Tiger habitat suitability. Despite a large suitable habitat for Sumatran Tiger (80.4%), the prey distribution range in GLNP is relatively narrow (48.6%), with only 40.3% of the area showing overlap. This highlights the vulnerability of prey availability and the need to boost prey populations to ensure the long-term survival of Sumatran Tigers in GLNP.

Key words: Big cats, ensemble model, Gunung Leuser National Park, maximum entropy, prey availability, random forest, species distribution modeling

Introduction

The Sumatran Tiger (*Panthera tigris sumatrae* Pocock, 1929) is one of six remaining tiger subspecies in the world, with its habitat spread across various regions of the island of Sumatra (Dinerstein et al. 2006; Liu et al. 2018).

This subspecies is recognized by conservation managers as a valid taxonomic unit for tigers on Sumatra Island, allowing it to be distinguished from the extinct tiger subspecies of Java Island (*Panthera tigris sondaica* Temminck, 1844) (Wibisono and Pusparini 2010; Wibisono et al. 2011; Forum HarimauKita 2019; Goodrich et al. 2022). In the 1970s, the population of Sumatran Tigers was around 1,000 individuals (Tilson 1999). However, presently, their population is estimated to be approximately 618 tigers, including ± 290 females, scattered in fragmented forests (Luskin et al. 2017). Sumatran Tiger population densities varied significantly, ranging from 1.2 to 2.0 tigers per 100 km^2, depending on habitat conditions and human impacts (Wibisono et al. 2009; Pusparini et al. 2018). Factors such as prey availability and habitat degradation contribute to this variation. These tigers are more commonly found in protected mountain and lowland forests, while populations outside conservation areas continue to decline (Sunarto et al. 2012).

Threats to Sumatran Tigers are increasing due to habitat fragmentation, poaching, conflict with humans (Linkie et al. 2008), declines in prey animal populations (Lubis et al. 2020), and climate change affecting the availability of suitable habitat (Mukul et al. 2019). Forest fragmentation has resulted in decreased gene flow and population densities (Murphy and Romanuk 2014; Thapa and Kelly 2017), especially in key species, which face serious risk of extinction (Córdova-Lepe et al. 2018; Scanes 2018; Lino et al. 2019). Human activities further marginalize these species, including the Sumatran Tiger (Nijman and Shepherd 2015), and result in conflicts with local inhabitants that can increase threats to their survival (Meijaard et al. 2018; Padalia et al. 2019; Pandong et al. 2019; Naha et al. 2020; Kuswanda et al. 2022).

Gunung Leuser National Park (GLNP) covers an area of 830,268.95 ha on the island of Sumatra, Indonesia. It is an important landscape for the protection of Sumatran Tigers (Wibisono et al. 2011), with a tiger population estimated at around 140 individuals, including ± 66 females (Saout et al. 2013; Cochard 2017; Luskin et al. 2017). GLNP provides diverse forest cover and serves as a significant provider of ecosystem services (Balai Besar TNGL 2019). The forests in GLNP have a high density of vegetation, abundant prey, and low human pressure, making it an ideal habitat for Sumatran Tigers. Although Sumatran Tigers rely mostly on natural forests, they also occasionally use oil palm and plantation forests, but in small proportions (Maddox et al. 2007; Sunarto et al. 2012). GLNP plays an important role in protecting a variety of endangered mammals, including the Sumatran Tiger (Cochard 2017), with habitats that range from lowland to montane forests (Dinerstein et al. 2006).

To support the effective conservation of Sumatran Tigers in GLNP, it is important to understand the distribution pattern and habitat preferences of this subspecies (Widodo et al. 2022). Besides environmental conditions and anthropogenic factors, the availability of prey animals also strongly influences the presence of tigers in a habitat (Ash et al. 2020). Despite living in fragmented habitats, Sumatran Tigers can still survive if there are enough food sources (Lestari 2006; Wibisono et al. 2011). Higher populations found in lowland forests and near rivers are suggested to be associated with prey availability (Pahlevi 2010; Putri 2010; Patana et al. 2021). Therefore, incorporating prey availability in understanding the distribution pattern or habitat selection for the Sumatran Tiger is crucial for conservation efforts.

Species distribution models (SDM) are common tools to study the distribution pattern of wildlife species and to support conservation management for threatened species. Several studies using SDM for Sumatran Tigers have been developed for various objectives and approaches (Suyadi et al. 2012; Priatna 2020; Rahman et al. 2022; Pudyatmoko et al. 2023), but only the study by Suyadi et al. (2012) incorporated the prey factor into their modeling. The present study investigated the influence of prey presence in the Sumatran Tiger distribution model using advanced machine learning algorithms. We leveraged the available data on prey and tiger presence from regular patrols in the GLNP then modeled each single prey species' distribution as possible predictors for SDM of the tigers. By modeling the distribution of Sumatran Tigers using these predictors and more advanced methods, it is hoped that more accurate information will be obtained to design more effective conservation strategies in the future.

Methods

Study location

The research was conducted in Gunung Leuser National Park (GLNP), which is a habitat for Sumatran Tigers and their prey, such as Lesser Mouse-deer (*Tragulus kanchil* Raffles, 1821), Barking Deer (*Muntiacus muntjak* Zimmermann, 1780), Sumatran Serow (*Capricornis sumatraensis* Bechstein, 1799), Wild Boar (*Sus scrofa* Linnaeus, 1758), and Sambar Deer (*Rusa unicolor* Kerr, 1792). The study area covered the GLNP area of 8,302.69 km^2 (Ministry of Forestry 2014) plus a buffer from the outermost side of the area boundary of 35 km. This radius was set to capture the closest environmental predictors outside the park boundary, including settlements, roads, cropland, plantations, and rivers. This avoided biasing the pixel values in the outer GLNP area of these predictor layers.

GLNP is administratively located in two provinces, namely Aceh (6,249.14 km^2) and North Sumatra (2,053.55 km^2). The GLNP area is crossed by the Cross-Sumatra Road, which connects the middle lane between the two provinces, and the Alas River, which extends from North to South following the Cross-Sumatra route. Forest cover in the GLNP area itself is still quite pristine and dominated by primary and secondary forests. The research site is dominated by such forest area, while outside GLNP, at the border up to a distance of 35 km from the outer boundary, the land has been converted into a mix of crop area, built area, and plantation forests (Fig. 1).

Presence data

A total of 6,386 Sumatran Tiger presence points were obtained, with a distribution covering the entire area of the Gunung Leuser National Park (GLNP) and its buffer zone (Fig. 1). The data were acquired from GLNP's monitoring programs during the 2021–2023 period and from field surveys carried out in June and August 2024. The unpublished data from GLNP were based on SMART patrol, camera traps, and reports from partner organizations, which were the Wildlife Conservation Society (WCS) Indonesia and the Leuser Conservation Forum (Forum Konservasi Leuser). The types of data used included direct observations, camera traps, and the discovery of indirect evidence such as feces, urine,

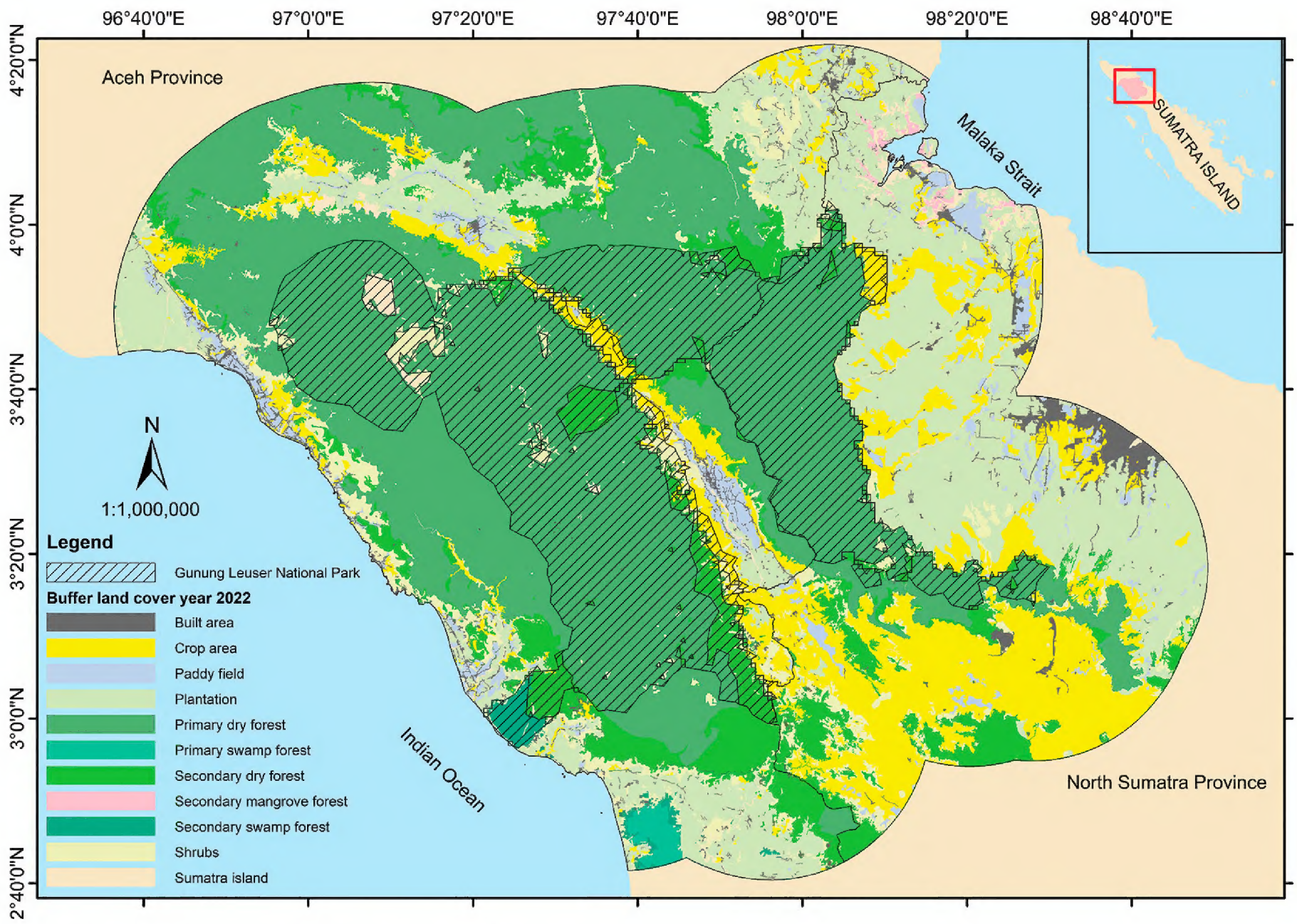

Figure 1. Research location in Gunung Leuser National Park.

hair, footprints, food remnants, claw marks, scratches, and ground scrapes (Hutajulu 2007; Sunarto et al. 2012) (Fig. 2). All data collected were compiled in the form of latitude and longitude coordinates, which were then used as input in species distribution modeling (Phillips et al. 2006; Franklin 2010).

The presence data on the main Sumatran Tiger prey, which were Lesser Mouse-deer (*T. kanchil*), Barking Deer (*M. muntjak*), Sumatran Serow (*C. sumatraensis*), Wild Boar (*S. scrofa*), and Sambar Deer (*R. unicolor*) (O'Brien et al. 2003; Allen et al. 2020), were also collected and compiled from the same sources as the Sumatran Tiger. The data of these prey species were also obtained from the Global Biodiversity Information Facility (GBIF) website (www.gbif.org), which provides occurrence data on species found in the study area (Nania et al. 2022; GBIF 2024). The data obtained were filtered to ensure their validity by selecting only the data recorded during the past ten years (2014–2024) and evaluating the evidence for the presence of the species and the accuracy of their coordinates. Data containing biased or inaccurate information were excluded to obtain valid prey-finding coordinate data that could be used in modeling. The amount of prey presence data used in the model is presented in Table 1.

Environmental variables

Environmental data were obtained from open-access sources (Table 2). These data were processed at a spatial resolution of 30 arc seconds (equivalent to 1 km) and encompassed the Gunung Leuser National Park (GLNP) with a terrestrial buffer area of 35 km from the park boundary. The uniform spatial resolution

Figure 2. Sumatran Tiger images captured from camera trap surveys (**a**) during The Gunung Leuser National Park monitoring program in 2023 and (**b**) during additional surveys in 2024. The arrow denotes the position of the tiger.

Table 1. Data sources and the number of prey animal presence points. Primary data were compiled from SMART Patrol 2021–2023 and field survey in 2024.

No.	Species	Primary data 2021–2024	Filtered GBIF data; DOI	Total Original presence data	Total presence data after spatial thining
1	*Capricornis sumatraensis*	13	5; https://doi.org/10.15468/dl.kpkxap	18	12
2	*Muntiacus muntjak*	83	1; https://doi.org/10.15468/dl.w8mn9y	84	61
3	*Rusa unicolor*	21	7; https://doi.org/10.15468/dl.zxrxec	28	20
4	*Sus scrofa*	53	2; https://doi.org/10.15468/dl.aaedw5	55	18
5	*Tragulus kanchil*	35	0; https://doi.org/10.15468/dl.my9359	35	17

and extent were set to avoid errors in modeling and provide optimal results in the model (Saputra and Lee 2021). The uniform resolution for all environmental data were determined based on the coarsest resolution among the available environmental data (Bucklin et al. 2014), which were the bioclimatic variables.

To select the variables used in modeling, a multicollinearity test was conducted to eliminate variables that exhibit high correlation. Multicollinearity will eliminate predictors with a Pearson correlation coefficient value (r) of more than 0.7 ($r > 0.7$) so that the variables used are free from bias (Dormann et al. 2012). Correlation is classified as high if it has a correlation coefficient $r \geq 0.70$; moderate (modest) if r is between 0.40–0.69; and low (weak) if $r < 0.39$ (Fowler et al. 1998). The results of this multicollinearity test were used to select the variables used as input in the species distribution analysis.

Table 2. Environmental data sources used in the analysis.

No.	Variables	Source or reference	Year
1	Elevation	SRTM elevation data from Worldclim website	1990–2000
2	19 bioclimatic varibles	Worldclim data (Fick and Hijmans 2017)	1990–2000
3	Distance to river	landscape of Indonesia (RBI)	2014
4	Distance to road	landscape of Indonesia (RBI)	2014
5	Distance to settlement	MoEF landcover map	2022
6	Distance to plantations	MoEF landcover map	2022
7	Distance to cropland	MoEF landcover map	2022
8	Soil type	FAO (Food and Agriculture Organization of the United Nations)	2007
9	Modified Normalized Difference Water Index (MNDWI)	Landsat 8	2022–2024
10	Soil-Adjusted Vegetation Index (SAVI)	Landsat 8	2022–2024
11	Enhanced Vegetation Index (EVI)	Landsat 8	2022–2024
12	Normalized Difference Vegetation Index (NDVI)	Landsat 8	2022–2024
13	Land cover	MoEF landcover map	2022

Species distribution model (SDM) approach

This research used two stages of modeling, namely the prey animal distribution model and then incorporating this into the Sumatran Tiger habitat suitability model. All variables were prepared in raster format with a spatial resolution of 30 arc seconds or equivalent to 1 km within a radius of 35 km from the GLNP boundary. The workflow of the analyses in this study are presented in Fig. 3.

Species distribution modeling (SDM) for prey and Sumatran Tiger suitability were conducted using the ENMTML package in R software (Andrade et al. 2020). This program was used to analyze the entire SDM process, including the provision of absence data. Pseudo-absence data was built with a combination method of environmental, geographic, and k-mean cluster constraints with a radius of 10 km (Senay et al. 2013).

To perform scatter analysis, two SDM algorithms, namely maximum entropy (MAXENT) (Phillips et al. 2006) and random forest (RF) (Liaw and Wiener 2002), along with a combination of those algorithms or ensemble model (ENS) (Araújo and New 2007; Marmion et al. 2009) were used. The selection of MAXENT and RF was based on their effectiveness in modeling ecological data, especially in complex landscapes such as tropical forests. MAXENT is widely used for presence-only data, which corresponds to occurrence data collected for both prey and predators, while RF is a non-parametric model known for its ability to handle large datasets and interactions between predictors. The ENS is commonly used to address the issue of uncertainty from a single algorithm (Araújo and New 2007; Marmion et al. 2009). The ENS model was formed through Principal Component Analysis (PCA) of all algorithm models then using the principal components as the final model (Thuiller 2004). A randomization technique was applied to divide the data into data for training and data for testing.

The best model from the three modeling methods was selected based on the highest value of performance evaluation. This model was then used for further analysis and to predict the distribution of the Sumatran Tiger. The model performance was evaluated by using five discrimination indices: area under the receiving operating characteristic curve (AUC) (Fielding and Bell 1997), Kappa coefficient

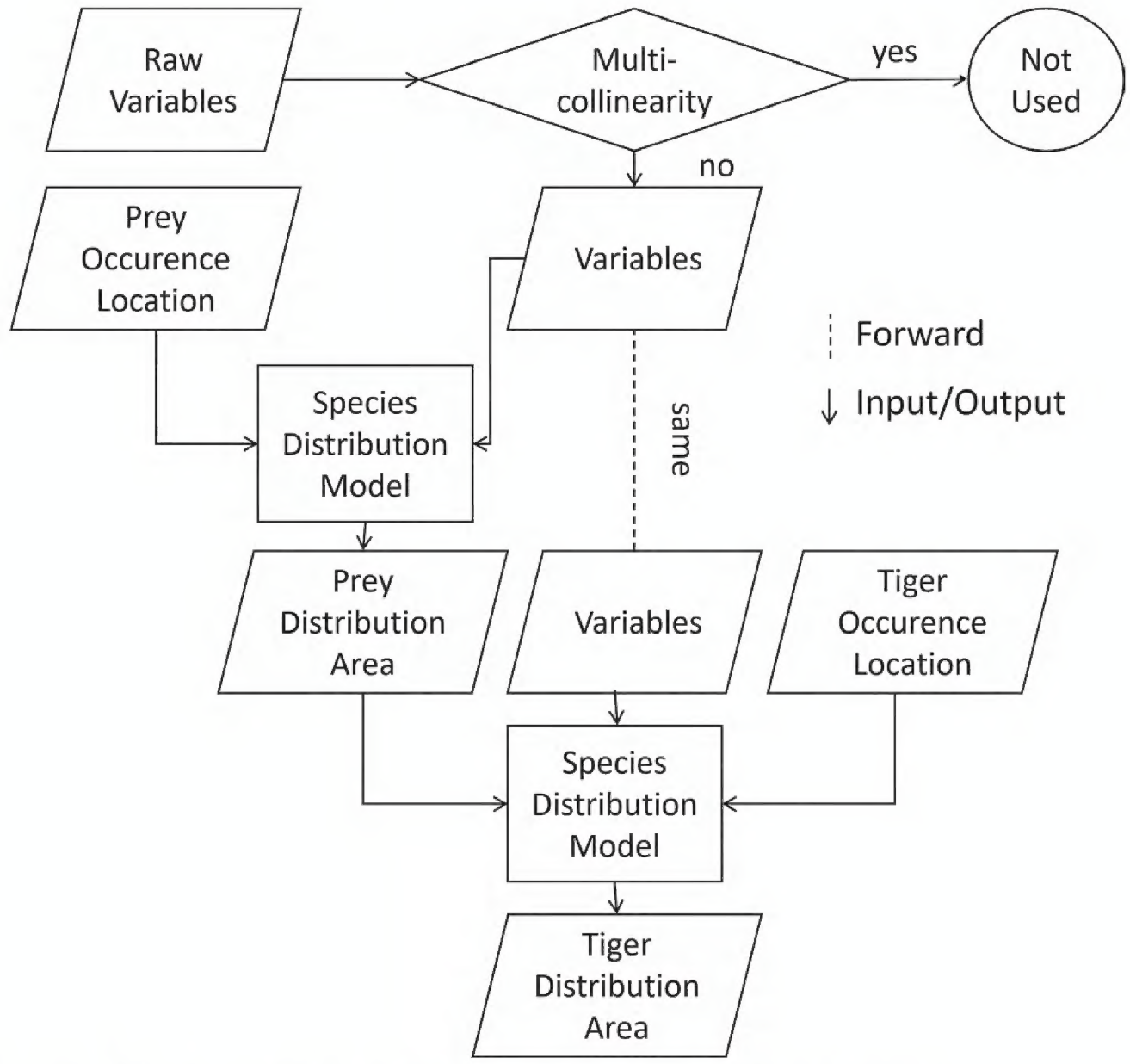

Figure 3. Flowchart of the distribution model for prey and Sumatran Tiger.

(Cohen 1960), the true skill statistic (TSS) (Allouche et al. 2006), Jaccard index, and Sørensen index (Leroy et al. 2018). The Sørensen method was used as a threshold application to produce a binary model of habitat suitability (suitable and unsuitable habitat) (Leroy et al. 2018). In addition to provide a more comprehensive assessment of model robustness for the best model, the sensitivity analysis of testing data was calculated from the confusion matrix for the best models only. Sensitivity analysis measures how well the model correctly predicts the presence of a species (true positive rate) (Fielding and Bell 1997; Guisan et al. 2017).

Results

Prey distribution model

The distribution model of five prey species was successfully built by using MAXENT, RF, and ENS. The best model from the three methods for each prey species was selected based on the highest value of the discrimination index (Table 3). The distribution model for *C. sumatraensis*, *M. muntjak*, *S. scrofa*, and *T. kanchil* were best performed by the RF algorithm, while for *R. unicolor*, the MAXENT algorithm performed best. Neither of the ENS models from the five prey species outperformed the single algorithm models. All the best models showed good performance with discrimination index values above 0.8, except the best model for *C. sumatraensis*, which showed a range value of 0.667–0.876 in five discrimination indices. The selected algorithm models of each prey species were then used as variable predictors along with other environmental variables to build the Sumatran Tiger distribution model.

Table 3. Discrimination index results from three SDM models for each type of Sumatran tiger prey animal in Gunung Leuser National Park.

No.	Prey Species	Algorithm	Discrimination Index				
			AUC	Kappa	TSS	Jaccard	Sorensen
1	*Capricornis sumatraensis*	MAXENT	0.317	0.200	0.200	0.570	0.721
		ENS	0.411	0.267	0.267	0.583	0.731
		RF	**0.856**	**0.667**	**0.667**	**0.800**	**0.876**
2	*Muntiacus muntjak*	MAXENT	0.904	0.813	0.813	0.841	0.913
		ENS	0.945	0.813	0.813	0.846	0.916
		RF	**0.953**	**0.851**	**0.851**	**0.861**	**0.924**
3	*Rusa unicolor*	**MAXENT**	**0.931**	**0.833**	**0.833**	**0.853**	**0.916**
		ENS	0.913	0.800	0.800	0.810	0.892
		RF	0.925	0.850	0.850	0.850	0.914
4	*Sus scrofa*	MAXENT	0.853	0.683	0.683	0.800	0.876
		ENS	0.888	0.850	0.850	0.870	0.921
		RF	**0.888**	**0.850**	**0.850**	**0.870**	**0.921**
5	*Tragulus kanchil*	MAXENT	0.767	0.633	0.633	0.700	0.823
		ENS	0.811	0.767	0.767	0.817	0.891
		RF	**0.933**	**0.933**	**0.933**	**0.933**	**0.960**

Notes: **bold** indicates the best performing algorithm based on the highest score of the five discrimination indices.

The most important variable determining the distribution model for each prey species was different (Table 4). Most species were strongly influenced by the annual temperature range. They were *C. sumatraensis*, *S. scrofa*, and *T. kanchil*. While *M. muntjak* was most influenced by seasonal rainfall and *R. unicolor* was most influenced by land cover. There was a consistent pattern regarding the relationship between annual temperature range and the presence of prey animals in the best models for all species (Fig. 4). An increase in the annual temperature range negatively affected the presence of prey animals in their habitat. However, after testing the multicollinearity of the five prey species along with other variable predictors, only three prey species were selected as they were not highly correlated with other variables. They were *R. unicolor*, *S. scrofa*, and *T. kanchil*.

Sumatran Tiger distribution model

The predicted distribution range or suitable habitat of the Sumatran Tiger in the GLNP from MAXENT and RF were very different, 2,042.83 km^2 from the MAXENT model and 6,754.25 km^2 from the RF model (Fig. 5) with similarly excellent model performances (> 0.9) (Fig. 6). The combination ENS model accounted for 6,672.11 km^2, close to the extent from the RF model (Fig. 5). The ENS model consistently outperformed the single algorithm models in all discrimination indices (Fig. 6). Therefore, for discussion of conservation implications, the ENS model was selected to represent the distribution range or suitable habitat of the Sumatran Tiger in the GLNP. In addition, the sensitivity analysis from the confusion matrix showed that the ENS model as the best model, exhibited a sensitivity of 0.986, indicating that 98.6% of true species presences were correctly identified. This suggests that the model was highly effective at minimizing omission errors (false negatives), which is critical for conservation planning (Fielding and Bell 1997).

Table 4. Importance value of variables for prey species distribution model (best algorithm) in Gunung Leuser National Park.

No	Variables	Importance value				
		***Capricornis sumatraensis* RF**	***Muntiacus muntjak* RF**	***Rusa unicolor* MAXENT**	***Sus scrofa* RF**	***Tragulus kanchil* RF**
1	Distance to settlement	0.06	0.217	0.162	0.05	0.051
2	Distance to cultivated land	0.105	0.033	0.125	0.078	0.131
3	Distance to river	0.019	0.038	0.027	0.035	0.019
4	Seasonal rainfall	0.124	0.309*	0.004	0.14	0.077
5	Wet quarter rainfall	0.118	0.067	0.028	0.151	0.121
6	Seasonal temperature	0.136	0.02	0.033	0.062	0.075
7	Annual temperature range	0.155*	0.03	0.141	0.298*	0.297*
8	Soil type	0.027	0.049	0.204	0.005	0.018
9	Land cover	0.03	0.116	0.224*	0.038	0.041
10	Modified normalized differenced water index	0.128	0.076	0.036	0.085	0.083
11	Soil-adjusted vegetation index	0.099	0.045	0.019	0.058	0.088

Notes: * variables that have the highest importance in the model.

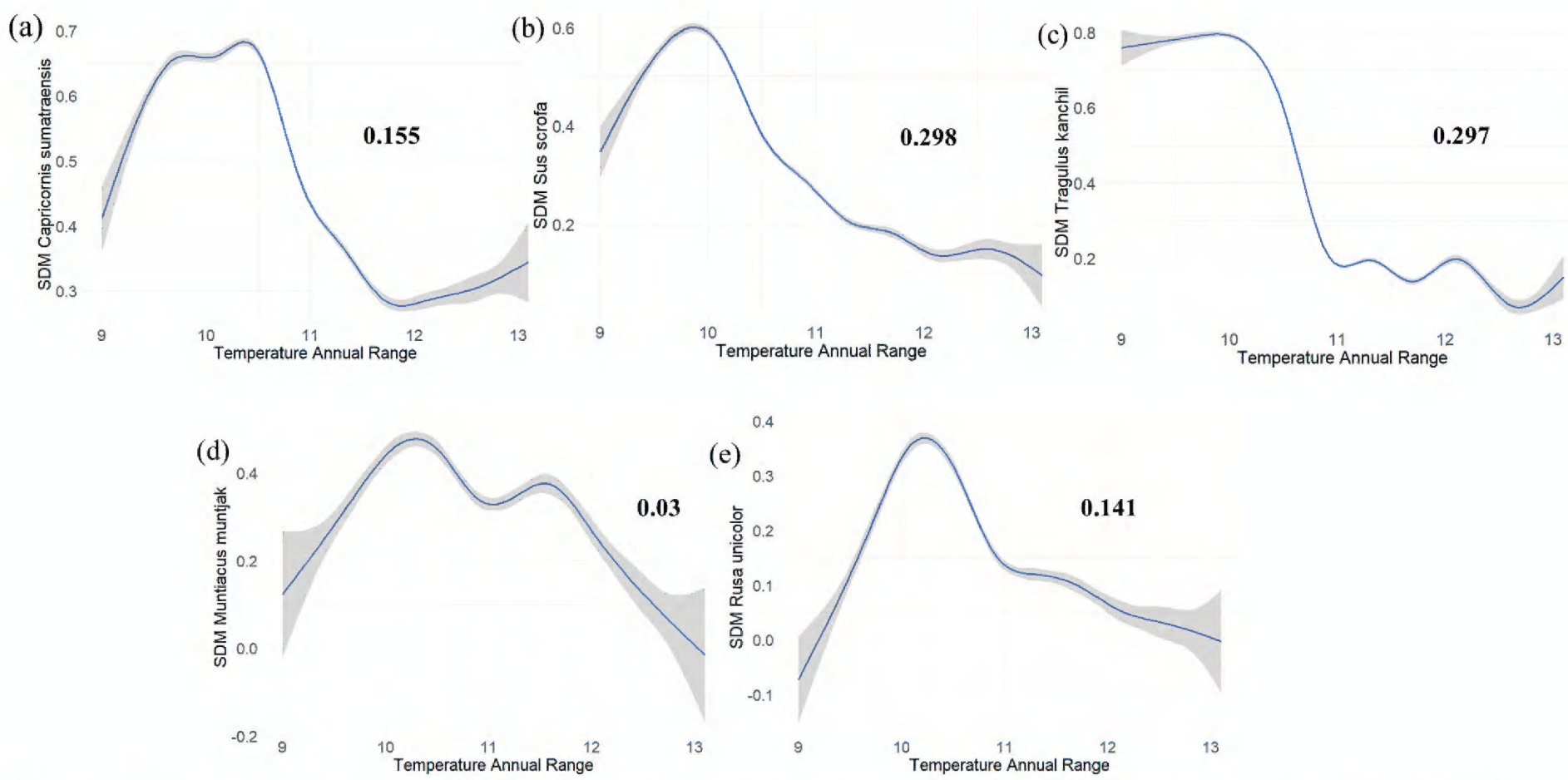

Figure 4. The response curve for the predictive presence of five prey species towards temperature annual range. The bold value represents the important value of the temperature annual range to the best model of each species. (**a–c**) are the model in which of temperature annual range was the most important predictor, while (**d, e**) are not.

The ENMTML package provides variable importance values only for models that use single algorithms (MAXENT and RF in this case), while such values are unavailable for the ENS model. Therefore, this study referred to the variable importances from the MAXENT and RF models. The variable importance analysis showed that the presence of prey significantly influenced the presence of Sumatran Tigers (Fig. 7), where the higher the probability of prey presence of *R. unicolor*, the higher the presence of the Sumatran Tiger. In addition, another determining variable was land cover, where primary and secondary forests were the most suitable land covers for tiger distribution range (Fig. 8). The curves showed that the presence of major prey animals, which were *R. unicolor*,

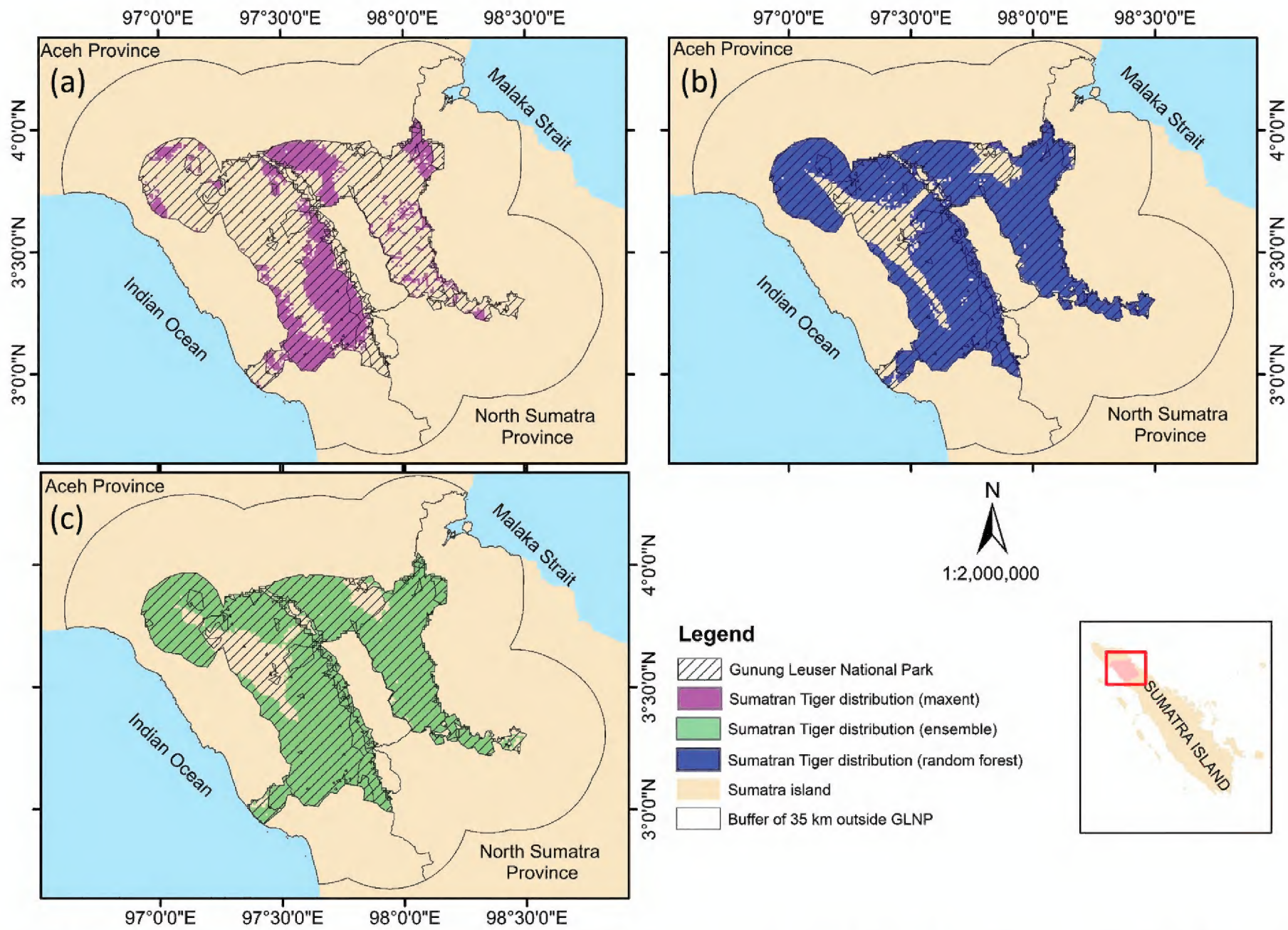

Figure 5. Predicted Sumatran Tiger distribution or suitable habitat analyzed using (**a**) maximum entropy, (**b**) random forest, and (**c**) ensemble of the two algorithms.

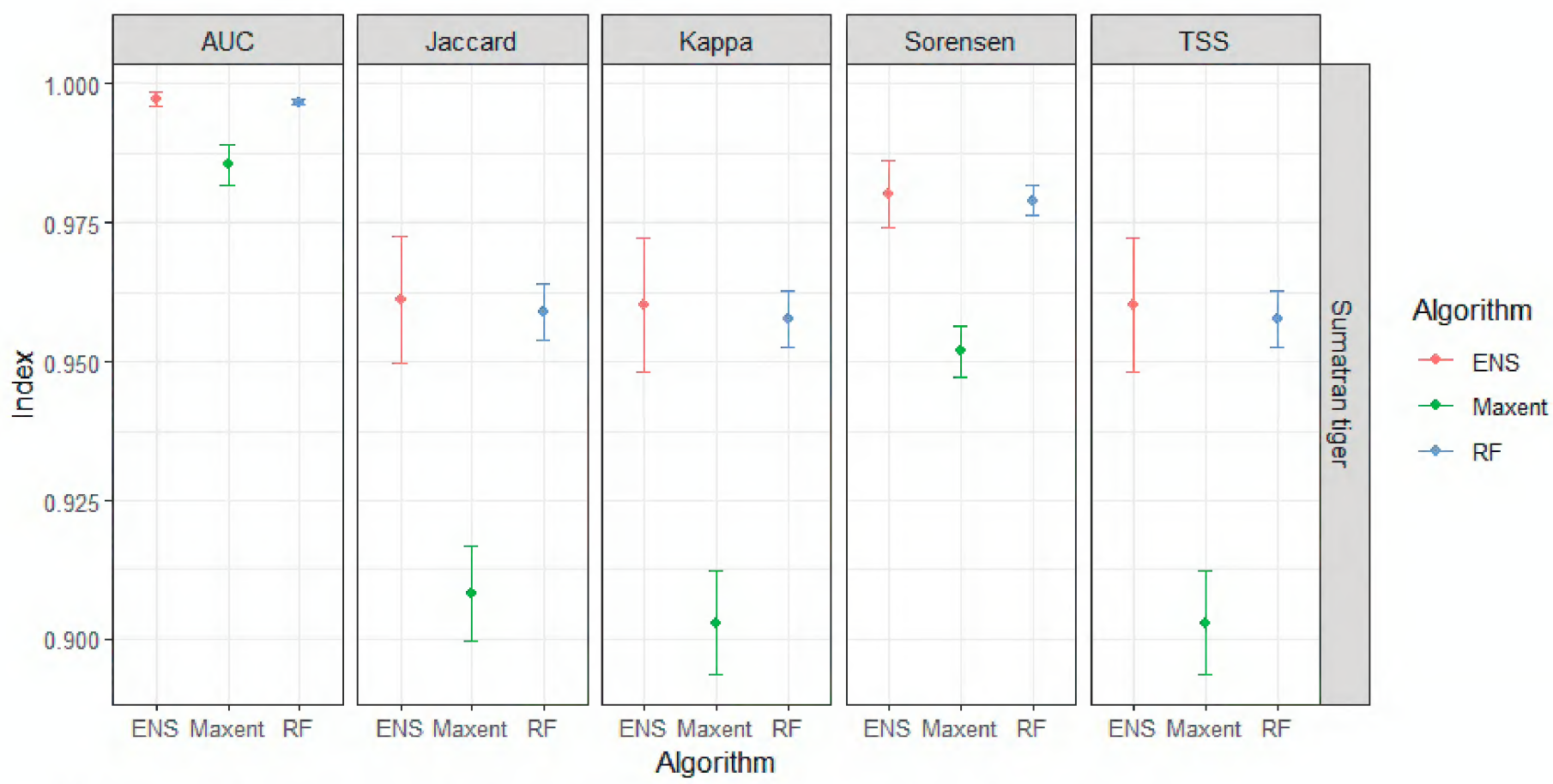

Figure 6. Evaluation for Sumatran Tiger distribution models using five discrimination indices.

S. scrofa, and *T. kanchil*, as well as forested land cover (primary and secondary forests), played an important role in determining the suitability of Sumatran Tiger habitat. Both algorithms showed a consistent pattern, where the presence of prey and forested land cover increased the probability of tiger presence.

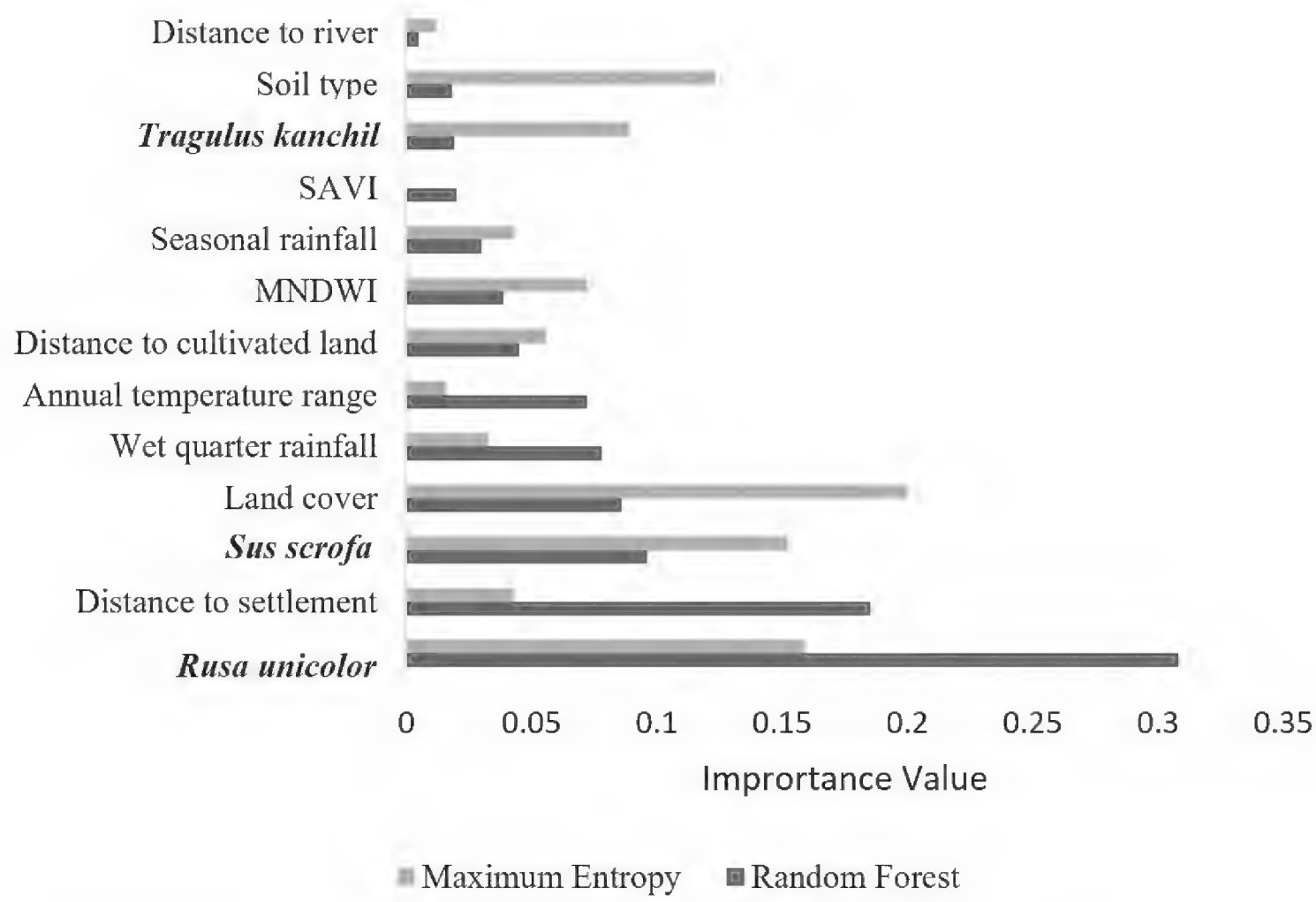

Figure 7. Importance value of variables for Sumatran Tiger distribution model. Bold indicates prey species with collinearity below 0.7. SAVI is the Soil-adjusted Vegetation Index. MNDWI is the Modified Normalized Differenced Water Index.

Overlapped distribution of tiger and prey

The suitable area for tiger prey species in the GLNP area was 48.6%, while the percent area of Sumatran Tiger distribution in the GLNP area was 80.4%, or about two times wider than the presence of prey (Fig. 9). The result of the overlapping analysis between the distribution of prey species and Sumatran Tigers was 40.3%.

Discussion

Prey distributions shape Sumatran Tiger distribution

The Sumatran Tiger is the top predator species in the GLNP. As a key species, its presence plays an important role in assessing forest ecosystem health in the GLNP area. Previous studies have analyzed the distribution of tigers using SDM that includes prey data, such as using the tiger density approach and the location of prey (Suyadi et al. 2012) and using prey density and environmental variables (Kina et al. 2020). This study focused on analyzing prey distribution as the initial stage of tiger distribution modeling. Prey played an important role in determining tiger distribution (Patana et al. 2021). The use of RF and MAXENT algorithms was a new method with multilevel analysis. Previous research used prey-finding data without in-depth prey distribution modeling (Suyadi et al. 2012). Our approach has proven to produce a better discrimination index compared to manual model building.

Our study highlights the crucial role of prey availability in shaping Sumatran Tiger distribution in GLNP. The Sumatran Tiger distribution model showed that *Rusa unicolor* and *Sus scrofa* were the most influential in the RF distribution model (Fig. 7), confirming that prey availability was a limiting factor for tiger populations. This result is consistent with previous research, which showed a close relationship between the density of prey animals and tiger presence

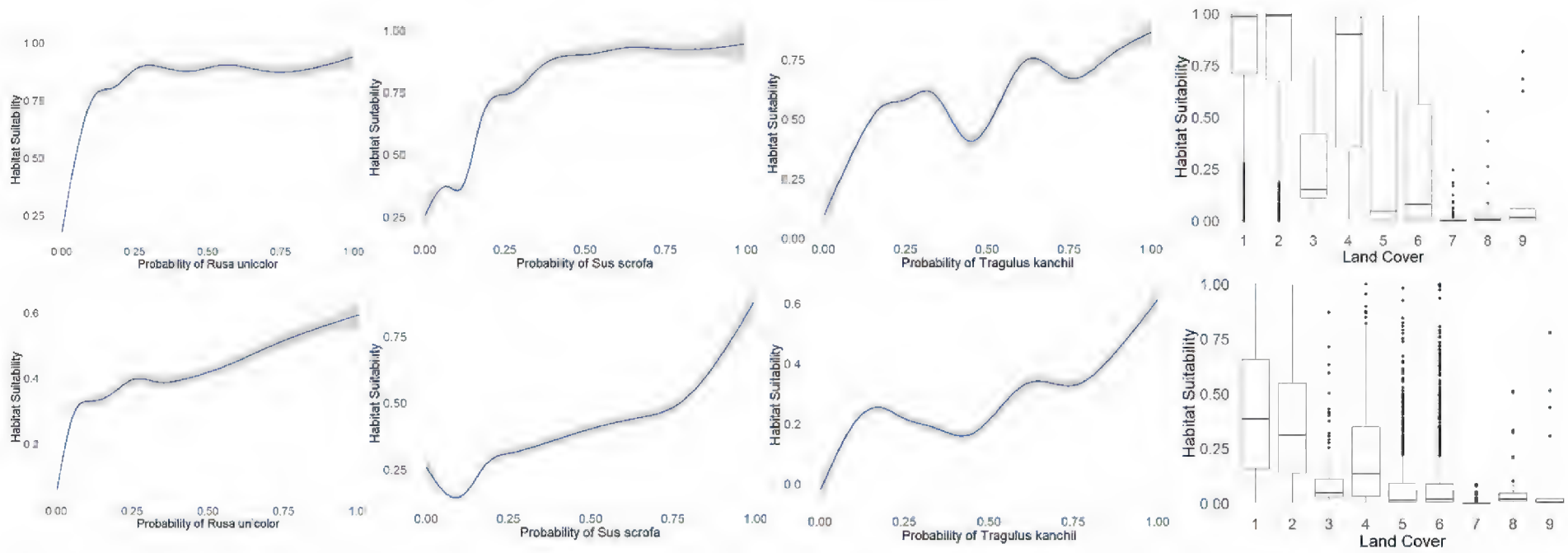

Figure 8. Analysis of the influence of prey and land cover variables on Sumatran Tiger's presence using random forest (RF) (top) and maximum entropy (MAXENT) algorithms (bottom). Land cover classes: 1. primary dry forest; 2. secondary dry forest; 3. swamp and mangrove forest; 4. grass and shrub; 5. plantation forest; 6. cultivated land; 7. settlement; 8. waterbody; 9. bare land.

(Hayward et al. 2012; Allen et al. 2020). The existence of Sumatran Tigers cannot be separated from the presence of prey animals. The relationship between prey distribution and tiger habitat suitability shows that increase in tiger habitat suitability corresponds with increase in prey presence, sequentially starting from *R. unicolor*, *S. scrofa* to *T. kanchil* (Fig. 8). Prey selection by tigers is based on the large biomass required to meet daily caloric needs, but it is not uncommon to prey on animals with small biomass when the presence of larger prey is reduced or difficult to obtain (Hutajulu 2007).

From a biophysical aspect, land cover and distance from settlements had a considerable influence on the distribution of Sumatran Tigers (Fig. 7). Sumatran Tigers preferred forested land covers and areas away from human activities (Hutajulu 2007). This is supported by our results, which show that land cover highly affected tiger distribution. The highest level of habitat suitability for Sumatran Tigers was in primary and secondary forests and far away from settlements (Fig. 8). The existence of dense natural forests in the GLNP area is an ideal habitat for Sumatran Tigers as it also provides ample habitat for their natural prey animals. Therefore, efforts to save the extent and to maintain the good quality of natural forest, are very important to reduce conflicts between tigers and humans, which often occur due to open access and land clearing close to tiger habitats (Tucker et al. 2018; Lubis et al. 2020).

Prey distribution models showed that climatic variables, especially annual temperature range, significantly affected the presence of several prey animals such as *C. sumatraensis*, *R. unicolor*, *S. scrofa*, and *T. kanchil*. Seasonal rainfall had a strong influence on *M. muntjak* (Table 4). An increase in the annual temperature range correlated with a decrease in the presence of prey animals (Fig. 4). Other research supports that rising temperatures could threaten the survival of *S. scrofa*, a mammal with a wide global distribution (Ruf et al. 2023). Increasing temperatures also lead to the loss of forested area due to fires and changes in the fruiting and flowering seasons of food plants (Measey 2010), which further increases the vulnerability of herbivores. Climate change also affects vegetation composition, which impacts the survival of wildlife in Indonesia's national parks (Sagala 2019).

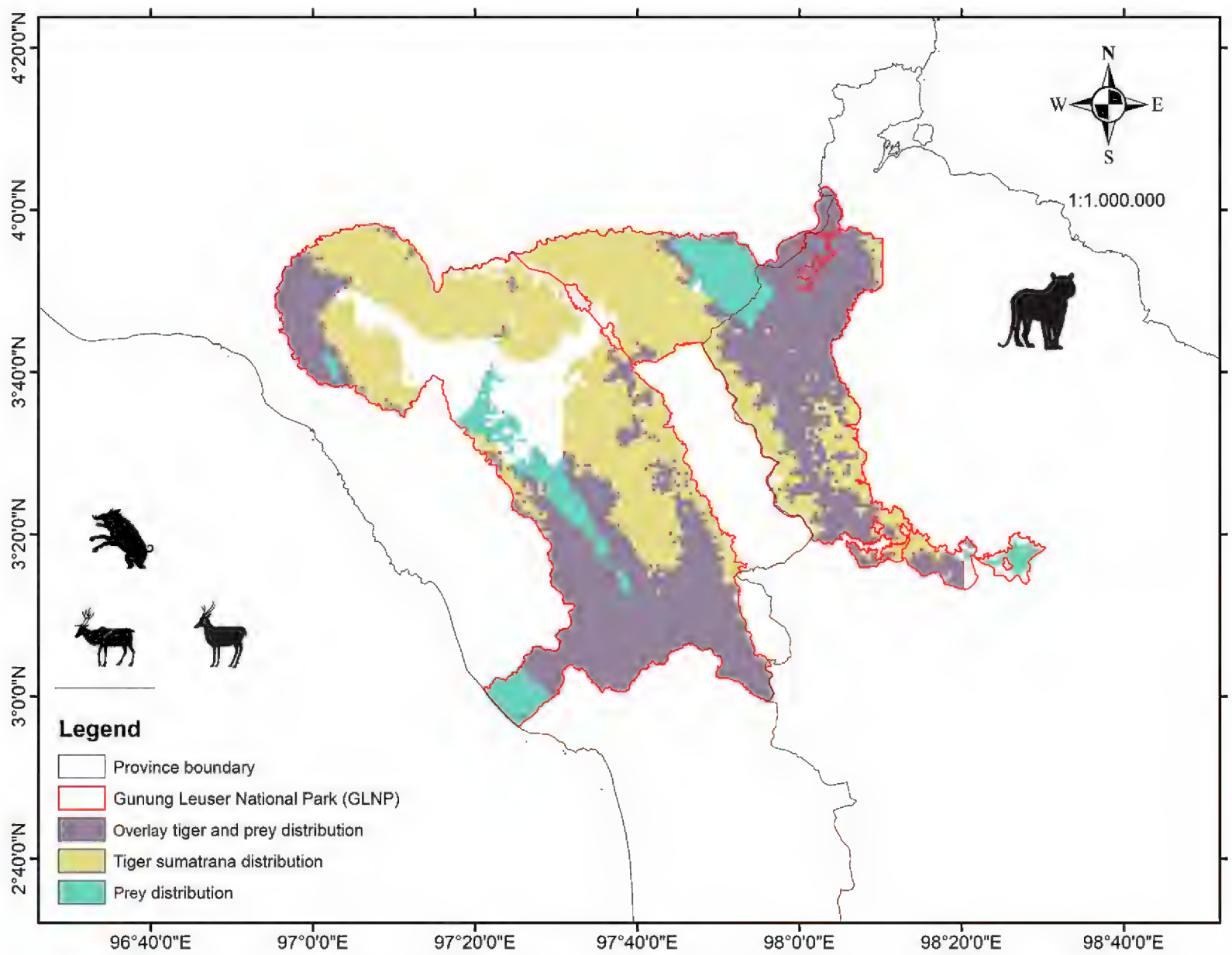

Figure 9. Map of the overlapping distribution of prey species and Sumatran Tigers (ENS) in Gunung Leuser National Park. Colored areas indicate areas of high habitat suitability for Sumatran Tigers and their prey animals, such as *R. unicolor*, *S. scrofa*, and *T. kanchil*. The 40.3% overlap between tiger and prey species suitability highlights the importance of areas with sufficient prey availability for tiger survival.

Thus, prey animals are vulnerable to future increases in temperature and rainfall expected from climate change (Mukul et al. 2019). Our study suggests that biophysical variables and prey availability directly influence the distribution of Sumatran Tigers, while bioclimatic variables primarily had an indirect effect through their influence on prey distribution. This suggests that climatic factors, such as annual temperature and seasonal rainfall, impacted the Sumatran Tiger distribution indirectly by shaping prey availability.

Model limitations

Our SDM framework acknowledges several sources of uncertainty, including algorithmic variability between MAXENT and RF. While spatial thinning reduced sampling bias in our occurrence data, residual uncertainty persists in under-surveyed regions (Kramer-Schadt et al. 2013). The integration of prey distributions, though ecologically justified (Karanth et al. 2004), introduced additional uncertainty as prey SDMs themselves contain estimation errors and may not fully capture predator-prey dynamics. Our ensemble approach helped mitigate these issues by identifying high-consensus areas (Araújo and New 2007), but we recommend these predictions be used cautiously in conservation planning, particularly in areas where prey data are limited.

In our study, some predictors could potentially have been prepared at a finer resolution, such as vegetation indices derived from Landsat data, which

have an original resolution of 30 meters. However, all environmental predictors were finally prepared at a spatial resolution of 1 km^2, which corresponds to the coarsest resolution among the datasets used—specifically, the bioclimatic variables from WorldClim (Fick and Hijmans 2017), which currently represent the finest bioclimatic data publicly available. While this resolution is commonly used in species distribution modeling and provides reasonable landscape-level insights, it may overlook fine-scale habitat preferences that are particularly relevant for wide-ranging species such as the Sumatran Tiger (Atzeni et al. 2020). Finer spatial resolution could potentially improve the model's ability to detect microhabitat features important for the species' occurrence. Given that different environmental variables might influence species distributions at different optimal scales or resolutions (Chen et al. 2023), future studies could consider employing a multiscale multivariate modeling framework (Atzeni et al. 2020; Penjor et al. 2021; Chen et al. 2023) to better account for the hierarchical nature of habitat selection and enhance the ecological realism of distribution models for the Sumatran Tiger.

Implications for Sumatran Tiger conservation

The potential distribution of Sumatran Tigers is still quite large in the GLNP forest area, with a suitable area of 80.4% of the total GLNP area. However, the potential distribution of prey only reached 48.6% of the GLNP area. The results of the overlap analysis between prey distribution, namely *R. unicolor*, *S. scrofa*, and *T. kanchil*, showed that only 40.3% can be accessed by tigers to obtain prey. These results indicate that it is important for policymakers to pay attention to the availability of prey to ensure the survival of Sumatran Tigers in the GLNP area. Food fulfillment for prey animals must be improved to preserve their populations in their natural habitat. Given the major influence of climate change on *S. scrofa* and *T. kanchil*, especially in terms of increasing annual temperatures, more conservation efforts are needed to protect these prey species. In addition, the influence of land cover on the presence of *R. unicolor* illustrates the importance of maintaining the current condition of forest stands for prey animals.

Our research emphasizes that prey population restoration should be the main focus of conservation strategies in GLNP. Strengthening populations of prey animals is an important step in maintaining Sumatran Tiger populations, as also recommended by a previous study (Lubis et al. 2023). The quality of vegetation in areas with low prey presence probability should be assessed and followed by restoration if the quality low. Increasing the effort of anti-poaching patrols inside the park and its surroundings could help prey animal population recovery (Karanth and Stith 1999; Goodrich 2010). Increasing prey availability in tiger habitats is an important preventative measure to reduce human-tiger conflict (Goodrich 2010).

Our study highlights that the area suitable for both Sumatran Tigers and their prey is much smaller than the area suitable for tigers alone. This suggests that the park's actual carrying capacity for tigers may be lower than predicted by considering habitat suitability on its own. The notably restricted predictive distribution range of prey species could be attributed to persistent hunting pressure surrounding GLNP (Figel et al. 2021, 2023), which may have compressed prey populations into smaller areas. While environmental factors such as land cover, distance to disturbances, and bioclimatic factors created favorable con-

ditions for tigers, the scarcity of prey appears to be the critical limiting factor for population growth. This finding supports established evidence that even high-quality habitats cannot sustain viable tiger densities when prey is depleted (Karanth et al. 2004). To refine these estimates, future studies should incorporate: (1) systematic prey density surveys across GLNP to better quantify prey-mediated carrying capacity, particularly in areas identified as suitable for tigers but currently lacking prey, and (2) assessments of anthropogenic pressures (e.g., poaching intensity) on prey distribution. Conservation efforts must adopt a dual approach: prioritizing habitat connectivity for prey recovery while simultaneously strengthening anti-poaching measures to mitigate human-induced prey (and tiger) scarcity (Linkie et al. 2015). Targeted interventions in areas where tiger habitat is optimal but prey populations are suppressed could unlock GLNP's full potential to support tiger population recovery.

Our study also highlights the potential impacts of climate change, particularly increased temperatures and seasonal rainfall, which could reduce habitat suitability for prey animals such as *S. scrofa*. Park managers should prioritize the protection of core forest areas and consider the translocation of prey animals from less fragmented habitats to buffer zones in GLNP. In addition, monitoring programs using camera traps and advanced remote sensing tools can help track prey and predator populations over time, ensuring adaptive management strategies.

Conclusion

Our study concludes that prey availability is the main factor limiting the distribution of Sumatran Tigers in GLNP. Although most habitat in GLNP are suitable for tigers, only some areas overlap with prey animal distributions. Environmental factors, such as forested land cover and distance from settlements, also affects tiger distribution. Therefore, conservation efforts should focus on increasing prey animal populations and restoring their habitat requirements.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: MHS, SW, WK, RTPN, and UMR. Methodology: MHS, SW, WK, and RTPN. Software: MSH and SW. Data curation: MHS, SW, WK, and HH. Data validation: HH. Formal analysis: MHS and SW. Investigation: MHS, SW, and WK. Resources: I. Writing – original draft: MHS and SW. Writing – review and editing: WK, RTPN, UMR, NA, RSN, AP, PP, AA, and I. Visualization: MHS and SW. Supervision: WK. All authors have read and agreed to the published version of the manuscript.

Author ORCIDs

M Hadi Saputra https://orcid.org/0000-0002-2928-7880
Salmah Widyastuti https://orcid.org/0000-0002-4073-8953
Wanda Kuswanda https://orcid.org/0000-0002-8496-3263
R. Taufiq Purna Nugraha https://orcid.org/0000-0003-4811-0332
Hendra Helmanto https://orcid.org/0000-0001-8538-9227
Agus Purwoko https://orcid.org/0000-0002-2237-245X
Pindi Patana https://orcid.org/0000-0001-6089-151X

Data availability

All of the data that support the findings of this study are available in the main text.

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